Food Avoidance Learning in Squirrel Monkeys and Common Marmosets

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Abstract

Using a conditioned food avoidance learning paradigm, six squirrel monkeys (*Saimiri sciureus*) and six common marmosets (*Callithrix jacchus*) were tested for their ability to (1) reliably form associations between visual or olfactory cues of a potential food and its palatability and (2) remember such associations over prolonged periods of time. We found (1) that at the group level both species showed one-trial learning with the visual cues color and shape, whereas only the marmosets were able to do so with the olfactory cue, (2) that all individuals from both species learned to reliably avoid the unpalatable food items within 10 trials, (3) a tendency in both species for quicker acquisition of the association with the visual cues compared with the olfactory cue, (4) a tendency for quicker acquisition and higher reliability of the aversion by the marmosets compared with the squirrel monkeys, and (5) that all individuals from both species were able to reliably remember the significance of the visual cues, color and shape, even after 4 months, whereas only the marmosets showed retention of the significance of the olfactory cues for up to 4 weeks. Furthermore, the results suggest that in both species tested, illness is not a necessary prerequisite for food avoidance learning but that the presumably innate rejection responses toward highly concentrated but nontoxic bitter and sour tastants are sufficient to induce robust learning and retention.

Introduction

For any organism to survive, it must have adaptive mechanisms to avoid toxicosis. This is particularly true for food generalists as many plants and animals are chemically protected against predation by slow-acting systemic poisons present in their tissues and body fluids (Bell and Charlwood 1980), thus making indiscriminate selection of potential food a considerable risk (Hughes 1990).

In mammals, a variety of behavioral and physiological mechanisms have been identified that allow food generalists to avoid being poisoned (Galef et al. 1994). First, there are innate rejection mechanisms such as the rejection of toxic materials that taste bitter to humans (Glendinning 1994); second, there are other physiologically adaptive responses such as vomiting or alterations in the digestion and processing of toxic materials (Le Magnen 1992); and third, there are learned aversions to distinctive foods if ingestion is followed by illness (Barker et al. 1977; Milgram et al. 1977).

Learning mechanisms seem particularly useful in tracking the permanent seasonal changes and variations in food composition and availability, and thus it is not surprising that the general ability to learn aversion to food has been demonstrated in a wide variety of species both in naturalistic settings and in laboratory experiments. In a series of landmark studies, Garcia and coworkers showed the rat to use primarily gustatory cues in the formation of poison-based aversions (Garcia 1989). The efficacy of stimulus classes other than taste in food avoidance learning appears dependent on the species and its ecological niche (Rozin and Kalat 1971). Although rats have shown that they are capable of associating visual or olfactory cues with illness with repeated trials, this learning is reportedly weak and, in the case of olfactory cues, needs to be combined with taste (Holder and Garcia 1987). In other species, however, nongustatory modalities may convey important food-related information. Avian species, for example, have repeatedly been shown to be able to rapidly associate a color stimulus, in the absence of taste cues, with illness (Wilcoxon et al. 1971; Roper and Marples 1997). Given

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the apparent reliance of birds on the visual modality in feeding, it seems reasonable to assume that the laws of learning for an animal are dependent on the demands of that particular animal's habitat and feeding habits (Nachman et al. 1977).

It is well established that primates, similarly to birds, possess highly developed visual systems (Fobes and King 1982) and that both human and nonhuman primates use visual as well as gustatory and perhaps other cues in food selection and rejection (Clydesdale 1993). The feeding behavior of frugivorous monkeys suggests that olfactory cues may also play a significant role in this context (Clutton-Brock 1977).

Surprisingly few studies, however, have so far examined food aversion learning in nonhuman primates (Riley and Tuck 1985), and the majority of these have either used this paradigm for assessing pharmacological drug discrimination (e.g., Glowa et al. 1991) or have concentrated on taste-based aversion learning (e.g., Bergman and Glowa 1986). In contrast, the ability of monkeys to use nongustatory cues in building associations between a potential food and its palatability has only rarely been investigated.

Given the presumed importance of visual and olfactory cues for food selection in frugivorous primates, it was the purpose of the present study to investigate food aversion learning in two species of New World monkeys that preponderantly feed on fruits and, in particular, to address the following questions: (1) Are squirrel monkeys (*Saimiri sciureus*) and common marmosets (*Callithrix jacchus*) able to reliably form associations between visual or olfactory cues of a potential food and its palatability? (2) Are they able to remember such associations over prolonged periods of time? (3) Are there differences between species in learning and memory performance and in salience of the cues?

According to the exploratory character of the study and a lack of information about appropriate dosage of the unconditioned stimulus (UCS) for the species under investigation, we decided to modify the classical conditioned food avoidance learning paradigm in one way: Instead of an illness-inducing drug like lithium chloride, we used a mixture of aversive-tasting, but nontoxic, substances (quinine hydrochloride plus ascorbic acid) as the UCS. This allowed us to additionally address the question of whether food avoidance learning in nonhuman primates also occurs in the absence of negative physiological consequences.

General Materials and Methods

SUBJECTS

Testing was performed using three male and three female adult squirrel monkeys and five male and one female adult common marmosets. The squirrel monkeys were housed as a social group in an enclosure composed of nine single cages (85 cm wide × 85 cm deep × 105 cm high) connected by sliding doors that could be closed to allow the temporary separation of animals for individual testing. The marmosets were housed separately in single cages (50 cm wide × 50 cm deep × 80 cm high). In both species, the design of the test cages prevented conspecifics from observing the animal under test.

All animals were born in captivity and had no previous experience with the method described below. Both species were maintained under a 12:12 hr light–dark schedule at 25°C and fed daily a diet of marmoset pellets (Altromin), fresh fruit, vegetables, and mealworms, with ad libitum access to water.

STIMULI

In all experiments, the animals were individually presented with pairs of cookies that only differed either in color or shape or odor, with one of the alternatives made unpalatable. The cookies were made of 50 grams of wheat flour, 10 grams of butter, and 1 spoonful of water. For the palatable cookies, 15 grams of sugar was added to the dough, and for the unpalatable cookies, 5 grams of quinine hydrochloride and 10 grams of ascorbic acid were added. The dough was rolled out, and the cookies were cut out round (diam., 0.5 cm) or triangle shaped (length of edge, 1 cm) and baked for 5 min at 140°C. Pilot experiments using conspecifics of the experimental animals showed that (1) only the combination of quinine hydrochloride and ascorbic acid reliably evoked aversive reactions, whereas cookies prepared with only one of these substances were less effective, and (2) the presence or absence of the aversive-tasting substances could not be detected visually or olfactorily as none of the four animals per species learned any discrimination, that is, reached the criterion of three consecutive correct choices within 10 trials (cf. Data Analysis) when presented with pairs of cookies that only differed in taste but were otherwise identical (both alternatives were round, unstained, and nonodorized).

For testing color as the discriminative stimulus, round cookies were stained red or yellow using odorless and tasteless commercial food dyes (Brauns-Heitmann, Warburg, Germany). For testing odor as the discriminative stimulus, round and unstained cookies were odorized by adding 1 ml of commercial baking aroma (almond or lemon extract, Dr. Oetker, Bielefeld, Germany) to the dough. For testing shape as the discriminative stimulus, unstained cookies without baking aromas were cut out round or triangle shaped.

A panel of human subjects was presented (1) with colored and (2) with odorized cookies and confirmed that (1) the food dyes were indeed odorless and tasteless and (2) the baking aromas were clearly perceptible and easy to discriminate by smell but altered the intensely sweet or bitter taste of the cookies only a little if at all. Furthermore, the animals showed no indication that the food dyes or the baking aromas affected the taste of the cookies as their behavioral reactions toward both the palatable and the unpalatable food items were unequivocal and identical to those shown in response to the differently shaped cookies that were neither stained nor odorized.

To get a further indication as to the perceptibility and discriminability of the odorants used, three squirrel monkeys were tested in a food-rewarded olfactory conditioning paradigm (Laska and Hudson 1993a) and distinguished easily between the odors of almond and lemon extract. Earlier studies have shown both species to be capable of perceiving and discriminating between the colors used here (Jacobs and Harwerth 1989).

PROCEDURES

In all experiments, three animals of each species were assigned to one combination of cue and UCS (e.g., red cookie palatable and yellow cookie unpalatable) and the other three to the alternative combination (e.g., yellow cookie palatable and red cookie unpalatable).

Pairs of cookies were presented in a rectangular dish of 30 × 10 cm mounted on the outside of the mesh of a test cage. To prevent animals from taking both cookies at the same time, the food items were placed 20 cm apart. The position of the cookies (e.g., yellow cookie presented left and red cookie presented right) was pseudorandomized to counterbalance possible position preferences. One pair of cookies was presented per animal and per day at 9 a.m., that is, 2 hr prior to feeding.

Three series of learning tests were performed consecutively and were followed by retention tests, taking care that only one task (i.e., one pair of cookies) per day was presented to the animals.

DATA ANALYSIS

In assessing performance, the animals' choice behavior in response to simultaneous presentation of the cookies was scored. Correct choices consisted in animals taking the palatable cookie as the first one into their mouth. Conversely, errors consisted in animals taking the unpalatable cookie as the first one into their mouth. Consumption or at least gustatory probing instead of grasping of a cookie was taken as the choice criterion as the inspection of the odorized cookies required an animal to grasp a cookie and guide it toward its nose. However, the sequence in which the cookies were grasped was also recorded in all experiments. Two-tailed binomial tests were performed to evaluate deviations from a chance distribution of choices.

Within-group comparisons across tasks were performed using the Friedman two-way analysis of variance (ANOVA). When ANOVA detected differences between tasks, this was then followed by pairwise Wilcoxon signed-rank tests for related samples to evaluate which tasks were responsible. Between-group comparisons within a given task were done using the Mann-Whitney *U* test for independent samples by converting the number of correct choices per animal and task into percentages (Siegel and Castellan 1988).

All data are reported as number of correct decisions per experimental condition and species or individual.

Experiment 1

This experiment was conducted to assess the ability of squirrel monkeys and common marmosets to reliably form associations between visual or olfactory cues of a potential food, in the absence of gustatory cues, and its palatability.

Materials and Methods

To familiarize the animals with the procedure and to control for possible spontaneous position preferences of individual animals in taking cookies, the experiment was preceded by a 7-day familiarization phase in which the monkeys were presented daily with one pair of identical, unstained, and nonodorized round cookies that both were palatable. At the end of this phase, all animals co-operated well and in no case showed significant position preferences.

On 10 consecutive days, the animals were then presented with one pair of cookies that only differed in color and palatability, and their choice behavior was recorded. Only when these 10 presentations were completed was the next series using differently shaped cookies started, which was finally followed by the third series of tests using differently odorized cookies.

On the very first presentation of each series (called day 0), all animals took and tasted both cookies owing to lack of any prior experience. The learning criterion for successful acquisition of an association between cue and palatability was set at three consecutive correct choices on the nine presentations (called days 1–9) following this probing trial.

Results

Table 1 summarizes the choice behavior of squirrel monkeys and common marmosets with color as the discriminative stimulus. At the group level, both species showed one-trial learning for this cue (two-tailed binomial test, $P < 0.05$), with five out of six *Saimiri* and six out of six *Callithrix* correctly choosing the palatable cookie at day 1, that is, on the first occasion after the initial presentation and probing of the alternatives at day 0. At the individual level, all animals from both species reached the learning criterion of three consecutive correct choices within the nine test trials. Whereas all six *Callithrix* reached criterion at day 3, that is, without making any mistake and thus as rapidly as possible, only four out of six *Saimiri* were able to do so, with the remaining two individuals reaching criterion at days 7 and 8. The total number of incorrect choices was six for the squirrel monkeys and one for the marmosets, and thus learning performance did not differ significantly between species (Mann-Whitney *U* test, $P > 0.1$).

Table 2 shows the choice behavior of squirrel monkeys and common marmosets with shape as the discriminative stimulus. At the group level, both species showed one-trial learning for this cue (two-tailed binomial test, $P < 0.05$), with five out of six *Saimiri* and *Callithrix* correctly chosing the palatable cookie at day 1, that is, on the first occasion after the initial presentation and probing of the alternatives at day 0. At the individual level, all animals from both species reached the learning criterion of three consecutive correct choices within the nine test trials. Five out of six *Callithrix* reached criterion at day 3, that is, as rapidly as possible, and the remaining marmoset at day 4. In contrast, only three out six *Saimiri* reached crite-

Table 1: *Choice behavior of squirrel monkeys and common marmosets with color as the discriminative stimulus*

	squirrel monkeys						common marmosets					
day	♂1	♂2	♂3	♀1	♀2	♀3	♂1	♂2	♂3	♂4	♂5	♀1
0	+	-	-	+	-	+	+	+	-	-	+	+
1	-	+	+	+	+	+	+	+	+	+	+	+
2	+	+	+	-	+	+	+	+	+	+	+	+
3	+	+	+	+	+	+	+	+	+	+	+	+
4	-	+	+	+	+	+	+	+	+	+	+	+
5	+	+	+	-	+	+	+	+	+	+	+	+
6	+	+	+	+	+	+	+	+	-	+	+	+
7	+	+	+	+	+	+	+	+	+	+	+	+
8	+	+	+	+	+	+	+	+	+	+	+	+
9	+	+	-	-	+	+	+	+	+	+	+	+

(+) A correct choice; (−) an incorrect choice. Correct choices consisted in animals taking the palatable cookie as the first one into their mouth; errors consisted in animals taking the unpalatable cookie as the first one into their mouths. On the very first presentation (day 0) all animals took and tasted both cookies. The shaded table cells indicate when an animal reached the learning criterion of three consecutive correct choices.

Table 2: *Choice behavior of squirrel monkeys and common marmosets with shape as the discriminative stimulus*

day	squirrel monkeys						common marmosets					
	♂1	♂2	♂3	♀1	♀2	♀3	♂1	♂2	♂3	♂4	♂5	♀1
0	-	+	-	+	+	+	-	+	+	+	-	-
1	+	+	+	+	-	+	+	-	+	+	+	+
2	+	+	+	+	+	-	+	+	+	+	+	+
3	+	-	+	+	+	+	+	+	+	+	+	+
4	+	+	+	+	-	+	+	+	+	+	+	+
5	+	-	+	+	+	+	+	-	+	+	+	+
6	+	+	+	+	-	+	+	+	+	+	+	+
7	+	+	-	+	+	+	+	+	+	+	+	+
8	+	+	+	-	+	+	-	-	+	+	+	+
9	-	-	+	+	+	+	+	+	+	+	+	+

Explanation as for Table 1.

rion without making incorrect choices, and the remaining three individuals reached criterion at days 5, 8, and 9, respectively. The total number of incorrect choices was 10 for the squirrel monkeys and 4 for the marmosets, and thus learning performance did not differ significantly between species (Mann-Whitney U test, $P = 0.06$) but showed a clear trend toward faster task acquisition by the marmosets compared with the squirrel monkeys.

Table 3 summarizes the choice behavior of squirrel monkeys and common marmosets with odor as the discriminative stimulus. At the group level, only the marmosets showed one-trial learning for this cue (two-tailed binomial test, $P < 0.05$), with five out of six individuals correctly chosing the palatable cookie at day 1, that is, on the first occasion after the initial presentation and probing of the alternatives at day 0. In contrast, only two out of six squirrel monkeys correctly chose the palatable cookie at day 1. At the individual level, all animals from both species reached the learning criterion of three consecutive correct choices within the nine test trials. Four out of six *Callithrix* reached criterion at day 3, that is, without making incorrect choices, and the remaining two marmosets at day 5. In contrast, only one out of six *Saimiri* reached criterion as rapidly as possible, with two of the remaining five individuals reaching criterion at day 4, two at day 6, and one at day 9. The total number of incorrect choices was 17 for the squirrel monkeys and four for the marmosets, and thus learning performance differed signifi-

Table 3: *Choice behavior of squirrel monkeys and common marmosets with odor as the discriminative stimulus*

day	squirrel monkeys						common marmosets					
	♂1	♂2	♂3	♀1	♀2	♀3	♂1	♂2	♂3	♂4	♂5	♀1
0	-	+	+	-	+	-	-	+	+	-	+	+
1	-	+	-	-	+	-	+	+	+	+	-	+
2	+	+	+	-	+	+	+	-	+	+	-	+
3	-	-	+	+	+	+	+	+	+	+	+	+
4	+	+	+	+	+	+	+	+	+	+	+	+
5	+	+	+	-	-	-	+	+	+	+	+	+
6	+	+	+	-	+	-	+	+	+	+	+	+
7	+	+	+	+	+	+	+	+	+	+	+	+
8	-	+	+	+	-	-	+	+	+	+	+	+
9	-	-	+	+	+	+	+	+	+	+	-	+

Explanation as for Table 1.

cantly between species (Mann-Whitney U test, $P < 0.02$).

A within-species comparison of learning performance in terms of number of days necessary for reaching the criterion across the three tasks indicates a nonsignificant (Friedman ANOVA, $P > 0.05$), but nevertheless quite consistent, tendency for quicker acquisiton of the visual cues compared with the olfactory cue in both species (Wilcoxon signed-rank tests, $P < 0.1$) as can be inferred from Tables 1–3. A comparison of the learning performance between species indicates a nonsignificant (Mann-Whitney U tests, $P > 0.05$) but consistent tendency for quicker acquisition and higher reliability of the aversion by the marmosets compared with the squirrel monkeys in all three tasks (cf. Tables 1–3).

Experiment 2

Experiment 1 showed both squirrel monkeys and common marmosets able to reliably form associations between visual or olfactory cues of a potential food, in the absence of gustatory cues, and its palatability. As this ability is only biologically meaningful if the animals are also able to retain these associations in memory and to make use of them in new encounters with the same stimuli, it was the purpose of this experiment to assess the ability of both species to remember such associations over prolonged periods of time.

Materials and Methods

Following the 10 consecutive presentations with a given stimulus combination in experiment 1, the animals were tested for retention of the learned associations by presenting them with the same pairs of cookies after noncumulative intervals of 3 days, 1, 2, and 4 weeks, and 4 months (i.e., 3, 10, 24, 52, and 172 days after training) and recording their choice behavior. After this first series of retention tests, all intervals were tested for a second time (i.e., 175, 182, 196, 224, and 344 days after training) with the exception of the 4-month interval that could only be tested with three out six animals per species on the second occasion.

Results

Table 4 summarizes the choice behavior of squirrel monkeys and common marmosets in the retention tests with color as the discriminative stimulus.

At the group level, both species showed significant retention for this cue at all intervals tested (two-tailed binomial test, $P < 0.05$), with only one or even no incorrect decision per interval and species occurring in the majority of cases. The total number of incorrect choices was six for the squirrel monkeys and two for the marmosets, and thus memory performance did not differ significantly between species (Mann-Whitney U test, $P > 0.2$).

At the individual level, all animals from both species showed significant retention, with none of the monkeys making more than 2 mistakes out of 9 or 10 decisions (two-tailed binomial test, $P < 0.05$). However, there was a nonsignificant tendency for higher reliability of retention in the marmosets compared with the squirrel monkeys, with five out of six *Callithrix* making no mistake at all, whereas only two out of six *Saimiri* chose correctly in all retention tests.

Table 4: *Memory performance of squirrel monkeys and common marmosets with color as the discriminative stimulus*

	Squirrel monkeys						Common marmosets					
Interval	♂1	♂2	♂3	♀1	♀2	♀3	♂1	♂2	♂3	♂4	♂5	♀1
3 days	++	++	++	++	+−	++	++	++	++	++	++	++
1 week	++	++	−+	+−	−+	++	++	++	−+	++	++	++
2 weeks	++	−+	++	−+	++	++	++	++	++	++	++	++
4 weeks	++	++	++	++	++	++	++	++	+−	++	++	++
4 months	+	+	+	++	++	++	+	+	+	++	++	++

(+) Correct choice; (−) incorrect choice. Correct choices consisted in animals taking the palatable cookie as the first one into their mouth; errors consisted in animals taking the unpalatable cookie as the first one into their mouth. Symbols indicate the response of an animal in the first and the second retention test, respectively (from *left* to *right*).

Table 5 shows the choice behavior of squirrel monkeys and common marmosets in the retention tests with shape as the discriminative stimulus.

At the group level, both species showed significant retention for this cue at all intervals tested (two-tailed binomial test, $P < 0.05$), again with only one or even no incorrect decision per interval and species occurring in the majority of cases. The total number of incorrect choices was four for the squirrel monkeys and three for the marmosets, and memory performance thus did not differ significantly between species (Mann-Whitney U test, $P > 0.2$).

At the individual level, all animals from both species showed significant retention, with none of the monkeys making more than 2 mistakes out of 9 or 10 decisions (two-tailed binomial test, $P < 0.05$). Reliability of retention was very similar between species, with three squirrel monkeys and four marmosets making no mistake at all.

Table 6 summarizes the choice behavior of squirrel monkeys and common marmosets in the retention tests with odor as the discriminative stimulus.

At the group level, the marmosets showed significant retention for this cue at all intervals up to 4 weeks (two-tailed binomial test, $P < 0.05$) and only failed with the 4-month interval. In contrast, the squirrel monkeys failed to show retention at the group level at all intervals tested (two-tailed binomial test, $P > 0.05$).

The total number of incorrect choices was 26 for the squirrel monkeys and 7 for the marmosets, and thus memory performance differed significantly between species (Mann-Whitney U test, $P < 0.01$).

At the individual level, all six *Callithrix* showed significant retention, with none of the marmosets making more than 2 mistakes out of 9 or 10 decisions (two-tailed binomial test, $P < 0.05$), whereas only one out of six *Saimiri* made less than three mistakes and thus performed above chance level.

General Discussion

The results of this study demonstrate (1) that both squirrel monkeys and common marmosets are able to reliably form associations between visual as well as olfactory cues of a potential food and its palatability, (2) that both species are able to remember the significance of the visual cues color and shape, even after 4 months, whereas only the marmosets showed retention of the olfactory cue for up to 4 weeks, and (3) a tendency for quicker acquisition and higher reliability of the aversion by the marmosets compared with the squirrel monkeys and a tendency in both species for quicker acquisition and higher reliability of the visual cues compared with the olfactory cue.

The ability to learn to avoid unpalatable food, as shown in the experiments reported here, may not seem surprising at first but rather, a necessary prerequisite for an animal to survive (Capaldi and Powley 1990; Le Magnen 1992). However, several aspects should be considered in evaluating the results of this study. First, the artificial test situation used here in which the animals had only one cue at a time at their disposal for distinguishing between palatable and unpalatable food is quite different from, and presumably more challenging than, natural circumstances. As animals generally tend to make use of all sensory information available in a given situation (Riesen 1982; Olton 1990), it seems reasonable to assume that this is also true for food avoidance learning and that they take advantage of

Table 5: *Memory performance of squirrel monkeys and common marmosets with shape as the discriminative stimulus*

	Squirrel monkeys						Common marmosets					
Interval	♂1	♂2	♂3	♀1	♀2	♀3	♂1	♂2	♂3	♂4	♂5	♀1
3 days	++	+−	++	++	++	++	++	++	++	++	++	++
1 week	++	−+	++	−+	++	++	++	−+	+−	++	++	++
2 weeks	++	++	++	++	++	++	++	++	++	++	++	++
4 weeks	++	++	++	++	++	++	++	++	+−	++	++	++
4 months	+	+	+	++	+−	++	+	+	+	++	++	++

Explanation as for Table 4.

Table 6: *Memory performance of squirrel monkeys and common marmosets with odor as the discriminative stimulus*

	Squirrel monkeys						Common marmosets					
Interval	♂1	♂2	♂3	♀1	♀2	♀3	♂1	♂2	♂3	♂4	♂5	♀1
3 days	++	−−	++	−+	−+	−+	++	++	−+	++	++	++
1 week	+−	−+	+−	−+	++	++	++	++	++	++	++	+−
2 weeks	++	−+	−+	++	−−	−−	++	−+	++	++	++	++
4 weeks	++	−+	+−	+−	−−	++	++	++	++	++	++	+−
4 months	+	−	+	−−	−+	−−	+	−	−	−+	++	++

Explanation as for Table 4.

a combination of cues for solving such problems whenever possible (Best et al. 1976). This supposition is supported by numerous studies on discrimination learning that showed nonhuman primates to perform better with a combination of cues than with cues presented singly (Harlow 1945; Warren and McGonigle 1969). Thus, we believe that the tasks used were not trivial at all. Rather, they allow us to positively answer the question of whether single features of a potential food are sufficient for food aversion learning in nonhuman primates.

Our finding of one-trial learning and robust retention of the visual cues color and shape, in both species tested, are in agreement with the apparent importance of the visual system for other aspects of primate behavior like spatial orientation or social interaction (Fobes and King 1982) and with reports on the role of visual information for food choice both in human (Clydesdale 1993) and nonhuman primates (Gautier-Hion et al. 1985; Regan et al. 1996).

The finding, however, that squirrel monkeys and common marmosets were also able to associate olfactory cues, in the absence of gustatory cues, with palatability of a potential food was somewhat unexpected. Although in recent years accumulating evidence suggests that both the olfactory performance of nonhuman primates (Laska and Hudson 1993a,b; Laska and Freyer 1997; Laska and Teubner 1998) and the significance of olfaction in regulating primate behavior (Epple et al. 1993; Laska and Hudson 1995) have been underestimated, olfactory cues are frequently thought to be largely ineffective in food avoidance learning unless when combined with taste (Nachman et al. 1977; Bernstein 1991; Chambers and Bernstein 1995).

Nevertheless, within-species comparisons across the tasks used here suggest that for both primate species tested, olfactory stimuli may not be as easily associable as visual cues. A comparison of learning and memory performance between squirrel monkeys and common marmosets further suggests that the former might be less prepared to rely on olfactory cues than the latter. Two caveats, however, should be applied with regard to the interpretation of the intra- and interspecific differences found: First, the relative salience of cues may depend on the specific test situation as, for example, the usefulness of color varies as a function of the degree of illumination. The experimental conditions used here clearly favored the use of visual cues as the discriminants were not only brightly illuminated but also placed such that the animals could view them from a distance, whereas the evaluation of the olfactory cues required close contact. Furthermore, in previous studies we could show that squirrel monkeys can readily acquire a food-rewarded olfactory discrimination paradigm (Laska and Hudson 1993a) and that—contrary to their performance in the present study—they are able to remember the significance of olfactory cues for at least 20 weeks (Laska et al. 1996).

Second, differences in temperament are more likely to account for the observed differences in performance between the two species and for the comparatively poor performance of the squirrel monkeys with the odorized cookies in particular. The marmosets approached all tasks deliberately, frequently showed vicarious trial-and-error behavior prior to deciding on one of the alternatives (Muenzinger 1938), and only rarely probed the unpalatable cookies. The squirrel monkeys, in contrast, were much more daring and almost never showed any sign of hesitation while choosing. Furthermore, they strongly tended to probe a cookie once they held it in their hands. This behavior might explain why *Saimiri* made many more mistakes with the odorized cookies than *Callithrix* as the inspection of these food items imperatively required an animal to grasp it and to lead it toward its nose.

Comparative investigations on discrimination learning in nonhuman primates showed squirrel monkeys generally to perform at least as well as Callitrichids (Meador et al. 1987) and thus lend further support to the interpretation that differences in temperament rather than in cognitive abilities or in the relative salience of cues may underlie the observed species differences in olfactory-based food avoidance learning.

Among the few studies that have used nonhuman primates as animal models for the investigation of food avoidance learning, even fewer have explicitly tested the general potency of single food characteristics to be used by a monkey for acquiring such an aversion. Using differently colored drinking tubes, Johnson et al. (1975) reported that vervet monkeys (*Cercopithecus pygerythrus*) showed one-trial color-cued aversion learning, and Domjan et al. (1982) showed that the same species could associate the shape of food with its palatability. In the only study on this topic so far, which used a New World primate species, Fairbanks (1975) presented spider monkeys (*Ateles geoffroyi*) with pieces of differently colored bread and observed that most of her animals learned to avoid the distasteful items after one or two trials. All these findings are in line with the present results. Other studies used the aspect of natural food items and thus a combination of visual cues with Japanese macaques (*Macaca fuscata*) and generally found one-trial learning (Hasegawa and Matsuzawa 1981; Matsuzawa and Hasegawa 1982, 1983; Hikami et al. 1990). These studies, however, did not control for the absence of gustatory cues during the formation of associations between a potential food and its palatability as their primary purpose was to assess the influence of exteroceptive factors on food avoidance learning. To the best of our knowledge, the present study is the first one to systematically use odor stimuli as cues for food avoidance learning in nonhuman primates, and the finding that both species tested were basically able to acquire olfactory-based food aversions suggests that this often neglected sensory modality merits further investigation in future studies on learning of food acceptance in monkeys.

A final aspect of the present study is the finding that squirrel monkeys and common marmosets learned to avoid unpalatable food without experiencing negative physiological consequences. In contrast to the vast majority of studies that used illness-inducing drugs like lithium chloride as the UCS, we used a combination of ascorbic acid and quinine hydrochloride that apparently taste aversive to the monkeys but are most likely nontoxic, at least in the concentrations used here. Both the animals used in the pilot experiments to establish the appropriate concentrations of the UCS and their conspecifics used in the critical tests were carefully monitored for signs of indisposition or symptoms of intoxication like diarrhea, vomiting, or altered behavior, but none of these were ever observed. This suggests that in both species tested, illness is not a necessary prerequisite for food avoidance learning but that the presumably innate rejection responses toward highly concentrated bitter and sour tastants (Glendinning 1994) are sufficient to induce robust learning.

Taken together, the results of the present study provide evidence of the ability of squirrel monkeys and common marmosets to make use of both visual cues and olfactory cues for food avoidance learning and thus may serve as a basis for future studies to help reveal which features of a fruit are actually used by frugivorous monkeys for food selection under natural circumstances.

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References

Barker, L.M., M.R. Best, and M. Domjan. 1977. *Learning mechanisms in food selection.* Baylor University Press, Waco, TX.

Bell, E.A. and B.V. Charlwood. 1980. *Secondary plant products.* Springer-Verlag, New York, NY.

Bergman, J. and J.R. Glowa. 1986. Suppression of behavior by food pellet-lithium chloride pairings in squirrel monkeys. *Pharmacol. Biochem. Behav.* **25:** 973–978.

Bernstein, I.L. 1991. Flavor aversion. In *Smell and taste in health and disease* (ed. T.V. Getchell, R.L. Doty, L.M. Bartoshuk, and J.B. Snow), pp. 417–428. Raven Press, New York, NY.

Best, P.J., M.R. Best, and G.P. Lindsey. 1976. The role of cue additivity in salience in taste aversion conditioning. *Learn. Motiv.* **7:** 254–264.

Capaldi, E.D. and T.L. Powley. 1990. *Taste, experience and feeding.* American Psychological Association, Washington, D.C.

Chambers, K.C. and I.L. Bernstein. 1995. Conditoned flavor aversions. In *Handbook of olfaction and gustation* (ed. R.L. Doty), pp. 745–773. Marcel Dekker, New York, NY.

Clutton-Brock, T.H. 1977. *Primate ecology: Studies of feeding and ranging behavior in lemurs, monkeys and apes.* Academic Press, London, UK.

Clydesdale, F.M. 1993. Color as a factor in food choice. *Crit. Rev. Food Sci. Nutr.* **33:** 83–101.

Domjan, M., V. Miller, and G.A. Gemberling. 1982. Note on aversion learning to the shape of food by monkeys. *J. Exp. Anal. Behav.* **38:** 87–92.

Epple, G., A.M. Belcher, I. Küderling, U. Zeller, L. Scolnick, K.L. Greenfield, and A.B. Smith. 1993. Making sense out of scents: Species differences in scent glands, scent-marking behavior, and scent-mark composition in the Callitrichidae. In *Marmosets and tamarins: Systematics, behavior, and ecology* (ed. A.B. Rylands), pp. 123–151. Oxford University Press, Oxford, UK.

Fairbanks, L. 1975. Communication of food quality in captive *Macaca nemestrina* and free-ranging *Ateles geoffroyi. Primates* **16:** 181–189.

Fobes, J.L. and J.E. King. 1982. Vision: The dominant primate modality. In *Primate behavior* (ed. J.L. Fobes and J.E. King), pp. 220–243. Academic Press, New York, NY.

Galef, B.G., M. Mainardi, and P. Valsecchi. 1994. *Behavioral aspects of feeding: Basic and applied research in mammals.* Harwood Academic Publishers, Singapore.

Garcia, J. 1989. Food for Tolman: Cognition and cathexis in concert. In *Aversion, avoidance, and anxiety* (ed. T. Archer and L.G. Nilsson), pp. 45–86. Lawrence Erlbaum, Hillsdale, NJ.

Gautier-Hion, A., J.M. Duplantier, and R. Quris. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* **65:** 324–337.

Glendinning, J.I. 1994. Is the bitter rejection response always adaptive? *Physiol. Behav.* **56:** 1217–1227.

Glowa, J.R., R.D. Jeffreys, and A.L. Riley. 1991. Drug discrimination using a conditioned taste-aversion paradigm in rhesus monkeys. *J. Exp. Anal. Behav.* **56:** 303–312.

Harlow, H.F. 1945. Studies in discrimination learning by monkeys. VI. Discriminations between stimuli differing in both color and form, only color, and only in form. *J. Gen. Psychol.* **33:** 223–235.

Hasegawa, Y. and T. Matsuzawa. 1981. Food-aversion conditioning in Japanese monkeys (*Macaca fuscata*): A dissociation of feeding in two seperate situations. *Behav. Neural Biol.* **33:** 237–242.

Hikami, K., Y. Hasegawa, and T. Matsuzawa. 1990. Social transmission of food preferences in Japanese monkeys (*Macaca fuscata*) after mere exposure or aversion training. *J. Comp. Psychol.* **104:** 233–237.

Holder, M.D. and J. Garcia. 1987. Role of temporal order and odor intensity in taste-potentiated odor aversions. *Behav. Neurosci.* **101:** 158–163.

Hughes, R.N. 1990. *Behavioral mechanisms of food selection.* Springer-Verlag, Berlin, Germany.

Jacobs, G.H. and R.S. Harwerth. 1989. Color vision in Old and New World primates. *Am. J. Primatol.* **18:** 35–44.

Johnson, C., R. Beaton, and K. Hall. 1975. Poison-based avoidance learning in nonhuman primates: Use of visual cues. *Physiol. Behav.* **14:** 403–407.

Laska, M. and D. Freyer. 1997. Olfactory discrimination ability for aliphatic esters in squirrel monkeys and humans. *Chem. Senses* **22:** 457–465.

Laska, M. and R. Hudson. 1993a. Assessing olfactory performance in a New World primate, *Saimiri sciureus. Physiol. Behav.* **53:** 89–95.

———. 1993b. Discriminating parts from the whole: Determinants of odor mixture perception in squirrel monkeys, *Saimiri sciureus. J. Comp. Physiol. A* **173:** 249–256.

———. 1995. Ability of female squirrel monkeys (*Saimiri sciureus*) to discriminate between conspecific urine odors. *Ethology* **99:** 39–52.

Laska, M. and P. Teubner. 1998. Odor structure-activity relationships of carboxylic acids correspond between squirrel monkeys and humans. *Am. J. Physiol.* (in press).

Laska, M., T. Alicke, and R. Hudson. 1996. A study of long-term odor memory in squirrel monkeys (*Saimiri sciureus*). *J. Comp. Psychol.* **110:** 125–130.

Le Magnen, J. 1992. *Neurobiology of feeding and nutrition.* Academic Press, San Diego, CA.

Matsuzawa, T. and Y. Hasegawa. 1982. Food-aversion conditioning in Japanese monkeys (*Macaca fuscata*):

Suppression of key-pressing. *Behav. Neural Biol.* **36:** 298–303.

———. 1983. Food-aversion learning in Japanese monkeys (*Macaca fuscata*): A strategy to avoid a noxious food. *Folia Primatol.* **40:** 247–255.

Meador, D.M., D.M. Rumbaugh, J.L. Pate, and K.A. Bard. 1987. Learning, problem solving, and intelligence. In *Comparative primate biology,* Vol. 2, Part B (ed. G. Mitchell and J. Erwin), pp. 17–83. Alan R. Liss, New York, NY.

Milgram, N.W., L. Krames, and T.M. Alloway. 1977. *Food aversion learning.* Plenum Press, New York, NY.

Muenzinger, K.F. 1938. Vicarious trial and error at a point of choice: A general survey of its relation to learning efficiency. *J. Gen. Psychol.* **53:** 75–86.

Nachman, M., J. Rauschenberger, and J.H. Ashe. 1977. Stimulus characteristics in food aversion learning. In *Food aversion learning* (ed. N.W. Milgram, L. Krames, and T.M. Alloway), pp. 105–131. Plenum Press, New York, NY.

Olton, D.S. 1990. Spatial perception: Behavioral and neural analyses. In *Comparative perception,* Vol. II (ed. W.C. Stebbins and M.A. Berkley), pp. 217–243. John Wiley & Sons, New York, NY.

Regan, B.C., F. Vienot, P.C. Charles-Dominique, S. Pfefferkorn, B. Simmen, C. Julliot, and J.D. Moloon. 1996. The color signals that fruits present to primates. *Invest. Ophthal. Vis. Sci.* **37:** 2997.

Riesen, A.H. 1982. Primate perceptual processes. In *Primate behavior* (ed. J.L. Fobes and J.E. King), pp. 271–287. Academic Press, New York, NY.

Riley, A.L. and D.L. Tuck. 1985. Conditioned food aversions: A bibliography. *Ann. N.Y. Acad. Sci.* **443:** 381–437.

Roper, T.J. and N.M. Marples. 1997. Odor and color as cues for taste-avoidance learning in domestic chicks. *Anim. Behav.* **53:** 1241–1250.

Rozin, P. and J.W. Kalat. 1971. Specific hungers and poison avoidance as adaptive specializations of learning. *Psychol. Rev.* **78:** 459–486.

Siegel, S. and N.J. Castellan. 1988. *Nonparametric statistics for the behavioral sciences.* McGraw Hill, New York, NY.

Warren, J.M. and B. McGonigle. 1969. Attention theory and discrimination learning. In *Animal discrimination learning* (ed. R.M. Gilbert and N.S. Sutherland), pp. 113–135. Academic Press, London, UK.

Wilcoxon, H.C., W.B. Dragoin, and P.A. Kral. 1971. Illness-induced aversions in rat and quail: Relative salience of gustatory and visual cues. *Science* **171:** 826–828.

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